

# 单穗升麻的柱头和雌配子体发育及胚胎发生

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## A study on the development of stigma and megagametophyte, and embryogeny in *Cimicifuga simplex* Wormsk

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**Abstract** This is one of a series of studies on the reproductive features in *Cimicifuga nanchuanensis* Hsiao, an endangered plant endemic to China, and *C. simplex* Wormsk, a closely related and widely spread species as a control. The present paper deals with the results of cyto-morphological observations on the megasporogenesis, the development of female gametophytes, and the embryogeny in *C. simplex*. Its anatropous ovules are bitegminous and crassinucellate. A megaspore mother cell undergoes meiosis to form a linear or T-shaped megaspore tetrad. The embryo sac is of Polygonum type. The three antipodal cells persist up to the globular stage of embryo development. Two polar nuclei fuse to form a secondary nucleus close to the chalazal end of the embryo sac and connect with antipodal cells before fertilization. The development of endosperm is of Nuclear type. Cellularization of nuclear endosperm initiates since early globular stage of the embryo development. Development of the embryo in *C. simplex* is of Onagrad type. *C. simplex* is dichogamous. Stigmatic papillae emerge on the 1st ~ 2nd day and they elongate into stigmatic hairs on the 3rd ~ 5th day after stamens withering. The great impact of the differences of the receptive period of stigmas and pollen viability between the two species on effective pollination and seed-setting rate is discussed.

**Key words** *Cimicifuga simplex* Wormsk; Megasporogenesis; Female gametophyte development; Embryogeny; Stigma development

**摘要** 单穗升麻的雌蕊群由 1~5 枚离生心皮组成。子房单室, 4~9 枚倒生胚珠, 双珠被, 厚珠心; 大孢子四分体呈线形或 T 形排列, 合点端一个具功能。胚囊发育为蓼型。成熟胚囊中 3 个单核反足细胞, 胞质浓密, 在球形胚时期尚能观察到其退化痕迹。极核融合早, 次生核位于合点端。胚胎发生为柳叶菜型; 核型胚乳。雄蕊凋谢后 1~2 天花柱顶端腹缝线周围出现乳突细胞, 雄蕊凋谢后 3~5 天延长成柱头毛。讨论了单穗升麻与南川升麻柱头可授期与花粉生活力的差异对传粉效果和结籽率的显著影响。

**关键词** 单穗升麻; 大孢子发生; 雌配子体发育; 胚胎发生; 柱头发育

本文为濒危植物南川升麻生殖特性系列研究(Qi et al., 1998; Zhang et al., 1997; Qi et al., 1997)的一部分。为了探讨南川升麻的濒危状态与其生殖特性之间的联系, 选择了它的近缘广布种单穗升麻(Xiao, 1997)作对照研究, 希望通过对两种植物生殖特性及其与环境相互关系的研究, 有助于揭示导致南川升麻濒危的环境因素和生活史的薄弱环

节。本文阐述单穗升麻的柱头发育、大孢子发生、雌配子体发育和胚胎发生。单穗升麻的花药和雄配子体发育将另文发表(Li *et al.*, 2000)。

此外,作为被子植物的原始类群,与被子植物中其它中等大小的科比较,毛茛科植物的胚胎学研究受到各国学者更多的重视。据报道(Tobe, 1995)毛茛科被研究过的属已超过半数,即 29 属(不包括星叶草属和独叶草属)。其中 16 属植物(包括升麻属的一些种)的胚胎学特征已有较全面和详细的研究(Ly, 1981, 1971; Tobe, 1974a, 1974b; Jalan, 1963; Earle, 1938; Lonay, 1901)。最近,又有南川升麻的生殖特性系列研究。本文丰富了升麻属的胚胎学资料,并对确定升麻属在毛茛科中的系统位置具有一定的参考价值。

## 1 材料和方法

供试材料采自四川省南川县金佛山洋芋坪和黄草坪,从自然生长植株上不同发育阶段的花中取出雌蕊,分别用 FAA、CRF-Ⅲ戊二醛等固定并保存。石蜡切片,依不同发育时期切片厚度为 6~10  $\mu\text{m}$ ;铁矾-苏木精染色,固绿或桔红 G-丁香油饱和液复染;在显微镜下观察并拍照。为观察柱头发育情况,从开放后不同时期的花中取出雌蕊,经戊二醛固定,各级丙酮脱水,临界点干燥,喷金后在扫描电镜下观察、拍照。

## 2 观察结果

单穗升麻为多年生草本植物,总状花序,不分枝或基部有少数分枝。每花序由数十至上百朵小花组成。7月初花蕾显现,8月上旬开始开花,8月下旬至9月上旬为盛花期,9月下旬花谢,10月中旬果实成熟,种子脱落。

### 2.1 柱头发育

单穗升麻开花时,花柱、柱头均不明显,花柱短,花柱顶端(柱头)光滑(图版 I:1)。开花后约 7 天,花药全部开裂,柱头开始向背缝线一侧弯曲,此时退化雄蕊分泌蜜汁最多。至开花后第 8 天,雄蕊脱落,花谢。约 1~2 天(即开花后 9~10 天)后柱头腹缝线两侧开始形成乳突细胞(图版 I:2,2A),有时可见乳突细胞上有少数花粉粒附着。再过约 2~3 天(开花后 11~13 天或雄蕊脱落后 3~5 天),柱头进一步伸长、弯曲,其上的乳突状细胞延长成柱头毛(图版 I:3,4),柱头毛间有花粉粒存在。此时退化雄蕊仍有蜜汁分泌,仍有昆虫访花。

### 2.2 大孢子发生和胚囊发育

单穗升麻的雌蕊群由 1~5(多为 2)枚离生心皮组成,单室子房,每室胚珠 5~9,边缘胎座,倒生胚珠。双珠被,厚珠心。雌蕊的发育落后于雄蕊。在小孢子母细胞时期,心皮的腹缝线处出现数个胚珠原基,以后逐渐长大,在表皮下分化出一个细胞核显著、体积增大的孢原细胞,同时,内珠被开始突起(图版 II:1),此时花药的发育已处于小孢子四分体时期。在切片中还观察到 1 例具 2 个孢原细胞的异常现象(图版 II:2)。孢原细胞进行一次平周分裂,形成周缘细胞和造孢细胞(图版 II:3),周缘细胞加入到珠心组织中,造孢细胞即行大孢子母细胞的功能(图版 II:4)。

单穗升麻的胚囊发育为蓼型。大孢子母细胞经减数分裂(图版 II:5,6)形成 4 个大孢子,外珠被在此时期形成。4 个大孢子直线或 T 形排列,其中珠孔端 3 个退化,合点端一

个具功能(图版Ⅱ:8,9),具功能大孢子体积增大,成为单核胚囊,单核胚囊经3次有丝分裂,形成八核胚囊(图版Ⅲ:1~4)。随后八核胚囊细胞化,在珠孔端分化出卵器,合点端分化出3个反足细胞,中间是中央细胞(图版Ⅲ:5)。卵器包括1个卵细胞和2个助细胞,3细胞在空间上呈现品字形排列。卵细胞核位于合点端,珠孔端被大液泡占据;与卵细胞相反,助细胞合点端具大液泡,细胞核与大部分细胞质位于珠孔端(图版Ⅲ:6,7)。随着胚囊进一步发育,卵细胞体积增大,助细胞珠孔端出现丝状器(图版Ⅲ:8)。中央细胞的两极核存在时间极短,很快融合成1个次生核,核大,核仁明显,与反足细胞相邻接(图版Ⅲ:9)。合点端的3个反足细胞呈三角形排列,单核,细胞核大,细胞质浓,细胞的珠孔端较合点端宽(图版Ⅳ:1)。此种状态可一直保持至受精之后,至球形胚时期,仍能观察到其退化的痕迹(图版Ⅳ:7,8)。此外,在观察中发现有4孢子胚囊类型:大孢子母细胞减数分裂后不形成壁,4个单倍体的大孢子核在共同的细胞质中(图版Ⅱ:7),表现正常,未见任何退化迹象,看来可发育成胚囊。由于在大量切片中未观察到不同于蓼型的成熟胚囊,推测此种四孢子胚囊可能按五福花型(Johri,1963)发育。

成熟胚囊时期,珠心由双珠被包被,珠孔仅由内珠被形成。内珠被由2层细胞、外珠被由4层细胞构成。随着胚囊发育,珠心细胞从珠孔端向合点端逐渐解体。

### 2.3 胚和胚乳发育

单穗升麻的双受精过程中精核与次生核的融合早于精核与雌性核的融合。合子经一段时间的休眠,体积增大、伸长,明显液泡化。大液泡位于珠孔端(图版Ⅲ:10)。单穗升麻的胚胎发育属柳叶菜型。合子的第一次分裂为横分裂,形成具顶细胞和基细胞的2-细胞原胚。顶细胞体积小,核大,液泡不明显;基细胞体积大,珠孔端具大液泡,核位于靠近顶细胞位置(图版Ⅳ:3)。随后顶细胞纵裂,基细胞横裂,形成T形4-细胞原胚(图版Ⅳ:4)。以后继续分裂,分别形成胚体和胚柄。胚柄由2列细胞构成(图版Ⅳ:5~8)。种子自然脱落时胚处于球形期(图版Ⅳ:9)。

单穗升麻的胚乳发育为核型。初生胚乳核不经休眠即进行第一次有丝分裂(图版Ⅲ:10),早于合子的第一次分裂。当合子进入第一次有丝分裂前期时,已有多数游离胚乳核形成(图版Ⅳ:2),胚乳核沿胚囊壁分布,包埋于共同的细胞质中(图版Ⅳ:4),每核内具4~6个核仁。当游离核及细胞质沿胚囊壁形成完整的一层时,在游离核之间几乎同时产生分隔,形成一层胚乳细胞(图版Ⅳ:5)。随后胚乳细胞继续分裂,逐渐充满整个胚囊(图版Ⅳ:7~8),当种子脱落时,与胚体相邻的胚乳细胞已经解体,为胚的发育提供营养(图版Ⅳ:9)。

## 3 讨 论

毛茛科植物的胚胎学特征时有报道(Tobe,1995,1974; Vijayaraghavan, Bhandari, 1970; Davis, 1966; Schnarf, 1931; Dahlgren, 1927)。毛茛科植物的雌配子体发育存在着明显差异,如:胚珠具单胞孢原和多胞孢原;单珠被和双珠被;薄珠心和厚珠心等。单穗升麻的孢原细胞除极少为二细胞外,多为单细胞、双珠被、厚珠心。大孢子四分体呈线形或T形排列,合点端一个具功能,这与同属的南川升麻完全相同(Qi *et al.*, 1997),而与 *C. acerina* 略有差异(Tobe, 1974a, 1974b)。后者的胚珠有薄珠心和厚珠心两种类型,薄珠心中具线形

大孢子四分体,厚珠心中则形成三分体,且以厚珠心三分体类型占优势。

与大多数毛茛科植物一样,单穗升麻的胚囊发育为蓼型。曾观察到一例四胞型胚囊,是否为五福花型还有待于进一步探讨,因在毛茛科中尚未见五福花型胚囊的报道(Tobe, 1995)。

雌配子体中值得特别注意的特征是具有增大而宿存的反足细胞。毛茛科植物中多数种具3个反足细胞,并普遍存在双核和多核现象(Tobe, 1995),单穗升麻也具3个大型反足细胞,但均为单核、宿存,并以此状态保持至胚胎时期,这种结构与胚囊营养物质的吸收、运输和贮存有关。这与南川升麻反足细胞的结构特点完全相同(Qi *et al.*, 1997),而同属的 *C. acerina* 和 *C. racemosa* 中增大且宿存的反足细胞多为双核(Tobe, 1974a; Earle, 1938)。有不少关于反足细胞在受精前后的形态学变化以及引起这些变化原因的研究(Patel, Cook, 1972; Tschermak-Woess, 1956; Hasitschka-Jenschke, 1959; Huss, 1906; Mottier, 1895),反足细胞的超微结构和多倍化机理的研究也有所报道(Turala, Wolanska, 1990; Bohdanowicz, Turala-Szybowska, 1987),升麻属植物的反足细胞也是今后深入研究的好材料。

与其它毛茛科植物相同的另一结构特点是,胚囊中两极核存在的时间极短,八核胚囊细胞化后,上极核移向下极核,两极核很快融合成次生核。次生核位于合点端,并与反足细胞相连。通常蓼型胚囊中,次生核位于胚囊中间或珠孔端。单穗升麻等毛茛科植物的次生核位置表现出其原始性。

与南川升麻相似又略有差异,单穗升麻也是雌雄蕊异熟。在单花的雄蕊凋谢后1~2天(开花后约9~10天)柱头上才出现乳突细胞,再过2~3天柱头乳突细胞延长成柱头毛。柱头乳突细胞出现后达到可授期,比南川升麻早两天左右。但在单花的盛开期(开花后4~7天)柱头表面已附着少数花粉。据测定,单穗升麻花粉的生活力可维持约6天,比南川升麻多1天。由于单穗升麻可授期离雄蕊脱落时间比南川升麻短,进入可授期前已附着于柱头的花粉就有较多受精的机会;同样,单穗升麻同株异花授粉的机会也大于南川升麻。据我们所做的单花和整个花序不去雄套袋实验,南川升麻不结实而单穗升麻有一定的结实率,说明在自然条件下南川升麻不能自花授粉而单穗升麻能够进行自花授粉(Qi *et al.*, 1997)。在自然环境遭受破坏,居群内开花植株减少和传粉媒介不足的条件,单穗升麻的传粉效果和结籽率远高于南川升麻就可以理解了。在我们检查过的有柱头毛的成熟胚珠切片中,观察到胚与胚乳的发育的频率很高,证明多数胚珠双受精已经完成,这一点与南川升麻形成明显对照。

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### 图版说明 Explanation of plates

图版 I 单穗升麻开花后柱头扫描电子显微镜相片 1. 开花后 8 天雄蕊脱落时的柱头, 乳突细胞尚未出现 ( $\times 145$ ); 2. 开花后第 9 天, 雄蕊脱落后 1 天, 柱头乳突细胞开始显现 ( $\times 100$ ), 柱头部位的局部放大见 2A ( $\times 120$ ), 示乳突细胞; 3. 雄蕊脱落后 3 天(开花后 11 天), 乳突细胞延长成柱头毛 ( $\times 115$ ); 4. 雄蕊脱落后 5 天(开花后 13 天), 柱头毛进一步延长 ( $\times 115$ )。

图版 II 胚囊纵切面 1~4. 珠孔端向右; 5~9. 珠孔端向下; 1~3. ( $\times 450$ )。1. 珠心表皮下的孢原细

胞,注意刚形成的内珠被原基(箭头);2.具2个孢原细胞(箭头)的胚珠;3.孢原细胞平周分裂产生周缘细胞和造孢细胞(箭头所示);4.大孢子母细胞( $\times 365$ );5.大孢子母细胞减数分裂中期I(箭头)( $\times 750$ );6.大孢子母细胞减数分裂后期I(箭头)( $\times 500$ );7.单穗升麻中罕见的四孢子胚囊,4个大孢子核在共同的细胞质中(1核落在相邻的另一切片上)( $\times 450$ );8~9.合点端一个具功能大孢子(箭头所示),珠孔端的3个大孢子(箭头)退化( $\times 500$ );8.示直线排列;9.示T形排列。

**图版 III** 胚囊纵切面,除图4(珠孔端向上)外珠孔端均向下 1.二核胚囊(箭头)( $\times 450$ );2.四核胚囊(珠孔端有一核在相邻切片上)( $\times 500$ );3~4.同一胚囊的两张连续切片,示在合点端和珠孔端刚形成的4核(箭头所示)( $\times 580$ );5.八核胚囊细胞化,极核(箭头)尚未融合( $\times 220$ );6~7.同一胚囊的两张连续切片( $\times 625$ );6.示珠孔端的卵细胞(箭头)和1个助细胞;7.示助细胞(箭头)和卵细胞;8.胚囊珠孔端的卵器及助细胞的丝状器(箭头所示)( $\times 350$ );9.胚囊合点端的反足细胞(箭头)和次生核(箭头所示)( $\times 220$ );10.处于休眠期的合子和第一次有丝分裂后期的初生胚乳核(箭头)( $\times 280$ )。

**图版 IV** 受精后的胚囊纵切面,珠孔端向下 1.宿存的反足细胞( $\times 220$ );2.合子(箭头)进入分裂前期( $\times 220$ );3.二细胞原胚(箭头)( $\times 260$ );4.四细胞原胚(箭头)及沿胚囊壁分布的胚乳核( $\times 170$ );5.游离核胚乳细胞化,形成一层细胞胚乳( $\times 170$ );6~8.早期球形胚(箭头),胚柄由2列细胞构成,胚乳细胞逐渐充满胚囊,反足细胞(箭头)退化(6. $\times 330$ ;7~8. $\times 65$ );9.种子自然脱落时,胚处于球形期,胚体周围的胚乳细胞逐渐被消耗( $\times 250$ )。

**Plate I** Scanning electron microscopic photos of the stigmas in *Cimicifuga simplex* after anthesis. 1. Papillae have not appeared yet on the stigma on the 8th day after anthesis when stamens shed ( $\times 145$ ); 2. Stigmatic papillae emerge on the 1st day after stamens shedding (the 9th day after anthesis) ( $\times 100$ ). Higher magnification can be seen in Fig. 2A, showing papillae ( $\times 120$ ); 3. On the 3rd day after stamens shedding (the 11th day after anthesis), papillae extend into stigmatic hairs ( $\times 115$ ); 4. Further elongation of stigmatic hairs on the 5th day after stamens shedding (the 13th day after anthesis) ( $\times 115$ ).

**Plate II** Longitudinal sections of embryo sacs. The micropylar ends of embryo sacs face the right sides in Figs. 1~4, while in Figs. 5~9, facing downwards (1~3,  $\times 450$ ). 1. An archesporial cell below the nucellar epidermic cells. Note the just emerging inner integument primordium (arrow-head); 2. Two archesporial cells (arrowhead) appearing in an ovule; 3. Archesporial cell divides periclinally and produces a parietal cell and a sporogenous cell (arrowhead); 4. Megaspore mother cell ( $\times 365$ ); 5. Megaspore mother cell at metaphase I (arrow) of meiosis ( $\times 750$ ); 6. Megaspore mother cell at anaphase I (arrow) of meiosis ( $\times 500$ ); 7. A seldom seen coenomegasporium with four nuclei (the 4th nucleus located on the neighbouring section) in *Cimicifuga simplex* ( $\times 450$ ); 8~9. A functional megaspore (arrow) in the chalazal end and three degenerate megaspores (arrowheads) in the micropylar end respectively ( $\times 500$ ); a linear megaspore tetrad in Fig. 8; a T-shaped megaspore tetrad in Fig. 9.

**Plate III** Longitudinal sections of embryo sacs, micropylar ends face downwards except Fig. 4 (the micropylar end faces upwards). 1. A 2-nucleate embryo sac (arrowhead) ( $\times 450$ ); 2. A 4-nucleated embryo sac (another nucleus in micropylar end located on an adjacent section) ( $\times 500$ ); 3~4. Two successive sections of an ovule, showing an 8-nucleate embryo sac. Four nuclei (indicated with arrowheads) are located at both ends of the embryo sac respectively ( $\times 580$ ); 5. A just cellularized 8-nucleate embryo sac, two polar nuclei have not fused (arrowhead) ( $\times 220$ ); 6~7. Two successive sections of an embryo sac ( $\times 625$ ): An egg cell (arrow) and a synergid are shown in Fig. 6, a synergid (arrowhead) and an egg cell in Fig. 7; 8. A mature embryo sac, showing the egg apparatus and the filiform apparatus (indicated with an arrow) of a synergid ( $\times 350$ ); 9. A mature embryo sac, showing antipodal cells (arrow) and a secondary nucleus (arrowhead) at the chalazal end ( $\times 220$ ); 10. A zygote at dormancy stage and the primary endosperm nucleus (arrowhead) at the anaphase of the 1st division of mitosis ( $\times 280$ ).

**Plate IV** Longitudinal sections of embryo sacs after fertilization with the downward micropylar ends. 1. Persistent antipodal cells ( $\times 220$ ); 2. A zygote at the prophase of mitosis (arrow) ( $\times 220$ ); 3. A 2-celled proembryo (arrowhead) ( $\times 260$ ); 4. A 4-celled proembryo (arrow) and the free endosperm nuclei scattering along the embryo sac walls ( $\times 170$ ); 5. A layer of cellular endosperm formed *via* the cellularization of nuclear endosperm ( $\times 170$ ); 6~8. Early stage of globular embryos (arrowheads) with their suspensors composed of 2 rows of cells. Note the degenerate antipodal cells (arrows) and the embryo sac is filled with cellular endosperm gradually (6.  $\times 330$ , 7~8.  $\times 65$ ); 9. Longitudinal section of a seed, showing the globular stage of embryo development at natural shedding. Note the digested endosperm around the developing embryo proper ( $\times 250$ )

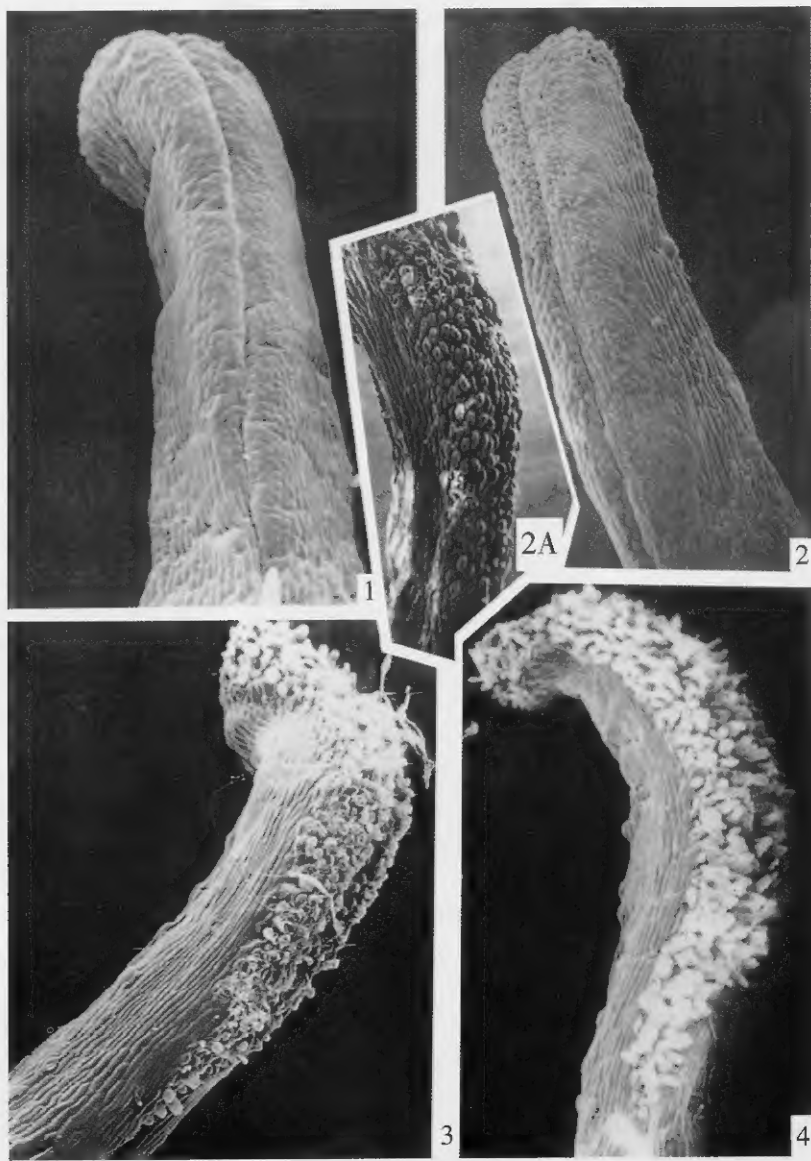
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陈晓麟等：单穗升麻的柱头和雌配子体发育及胚胎发生

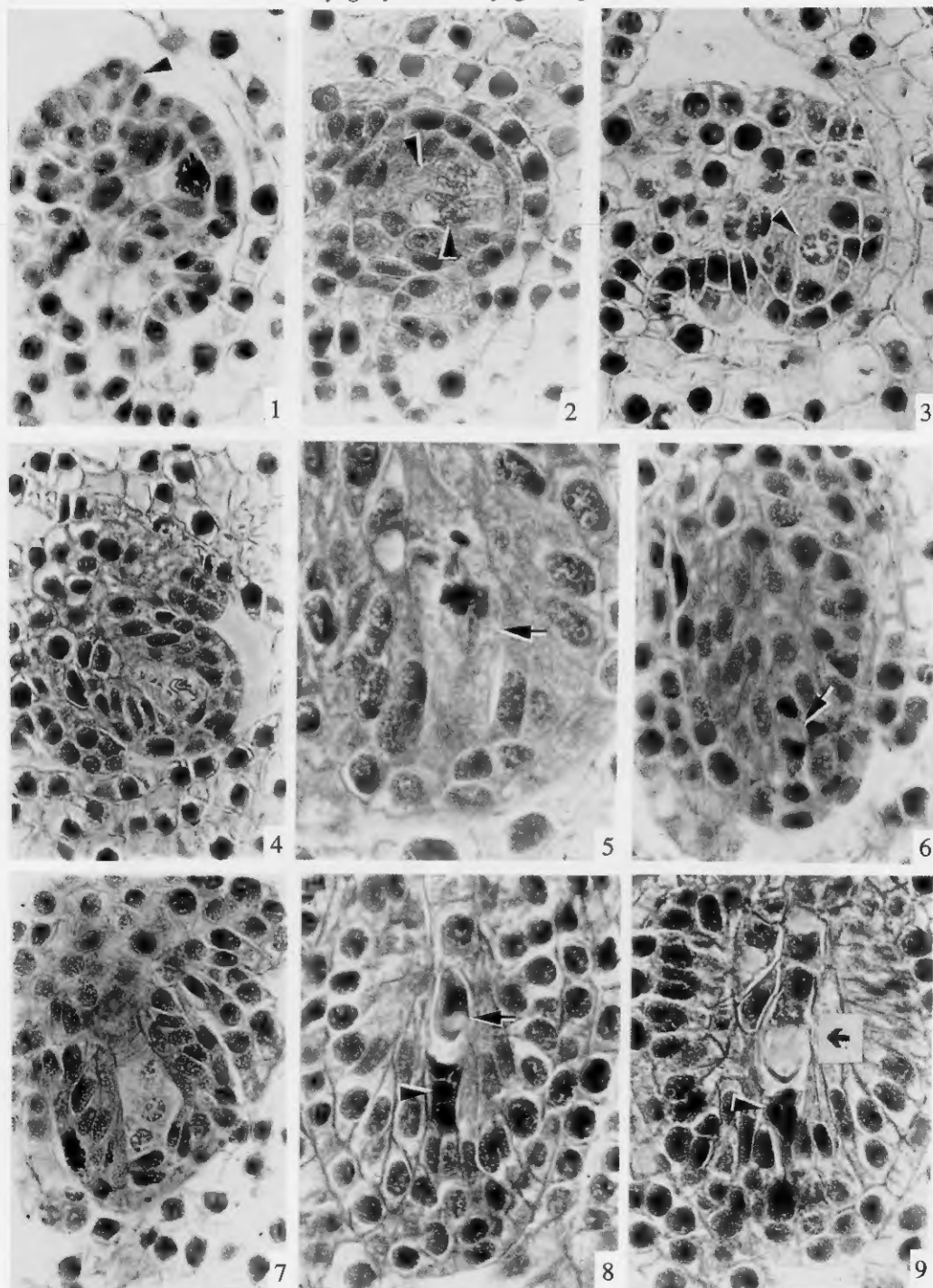
图版 I

CHEN Xiao-Lin *et al.*: A study on the development of stigma and megagametophyte,  
and embryogeny in *Cimicifuga simplex* Wormsk

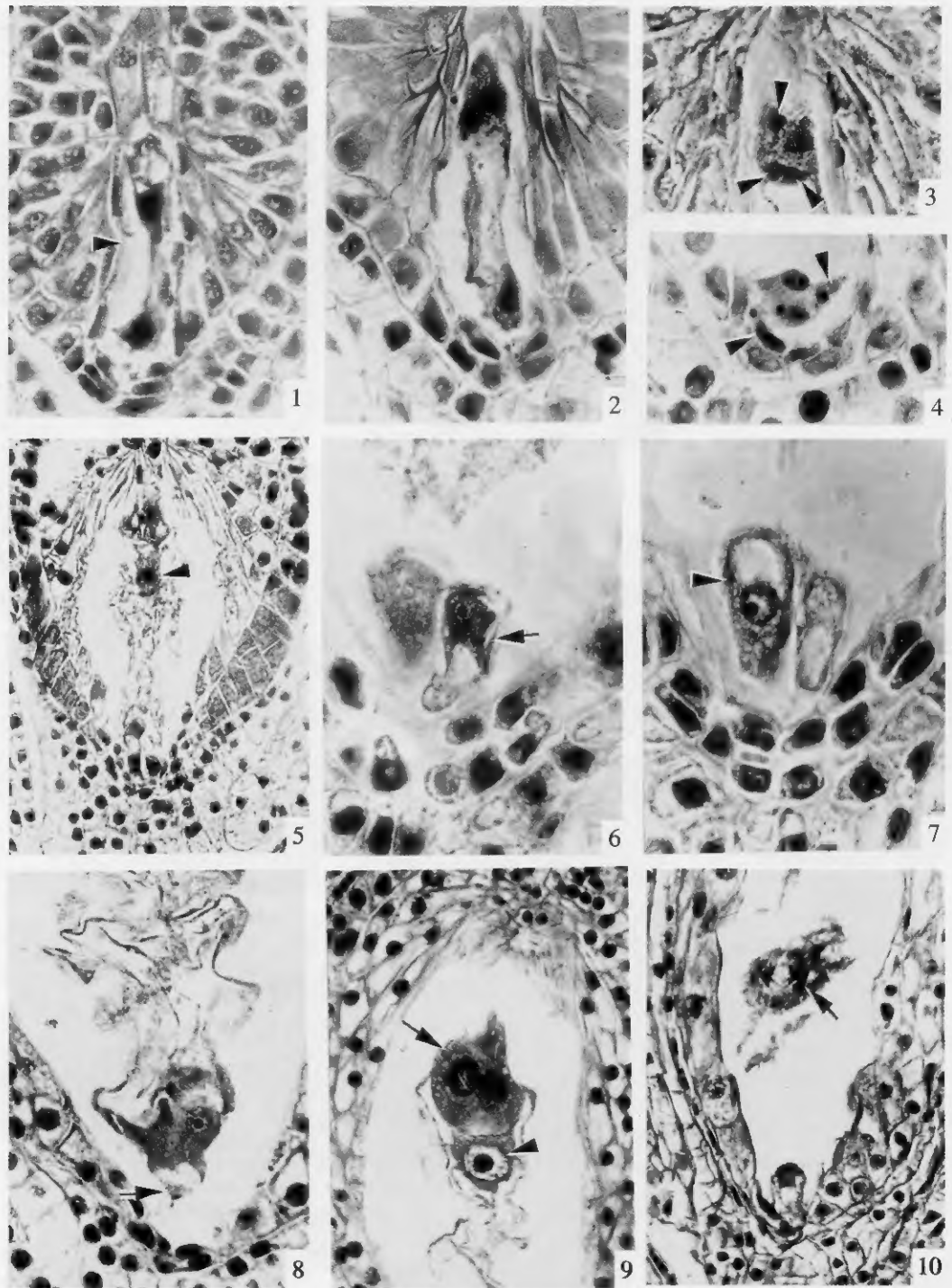
Plate I



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